DISPLACEMENT OF ONE TAXON BY ANOTHER AS THE CAUSE OF CERTAIN ECOLOGICAL SHIFTS IN *EUSTILICUS* SHARP (COLEOPTERA: STAPHYLINDAE): A TEST OF THE EVIDENCE

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Abstract.—A cladistic randomization test (Liebherr and Hajek 1990) is used to show that when the habitat preferences, altitudinal range, forest preferences, and body size of species of *Eustilicus* are mapped onto a phylogeny for the genus, the resulting patterns deviate statistically from patterns generated at random, even though the character consistency indices for these traits are low. Generally, the results of the test are consistent with the premise that many ecological shifts in *Eustilicus* have taken place through the displacement of one taxon by another. However, some species have broad ecological preferences; interpretation of test results which take this into account is problematic. When the randomization test is carried out at subordinate taxonomic levels in the genus, some ambiguities in the test are revealed; it is necessary to refer to the original data to resolve the difficulties.

Key Words: taxon displacement, taxon cycle, taxon pulse, ecological shift, randomization test

The staphylinid beetle genus *Eustilicus* Sharp comprises about 102 species, most of which live in montane forests between 800 and 3000 m elevation in litter of one kind or another (Frania 1990; manuscript in preparation). Larvae and adults occur in the same habitat, are general predators, and attain a length of 5–10 mm. The range of the genus extends from the eastern and southwestern United States to Bolivia and southeastern Brazil, but is centered upon Mexico and Guatemala; about 71 species are confined to this area.

In a taxonomic revision of *Eustilicus,* a hypothesis of phylogeny for 91 of the species was developed using morphological characters (Frania 1990, manuscript in preparation). Eight monophyletic groups were recognized, the largest being the cras-

sidens group[1] with 62 species. Each species group was found to exhibit a distinctive array of natural history traits. To determine how changes in ecological preference took place in this genus, some ecological attributes of the species were mapped in various ways onto the phylogeny (e.g. Fig. 1). It was concluded that many of the shifts in habitat type, altitudinal range, and forest preference which took place in *Eustilicus* were owing to the displacement of one taxon by another. In particular, the crassidens group displaced all the other groups (including the

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[1] Species group names are not italicized in the text in order to emphasize that these names are being used informally. Also, species are referred to by number rather than by name. This is because many of the species are new and the revision has not been published.
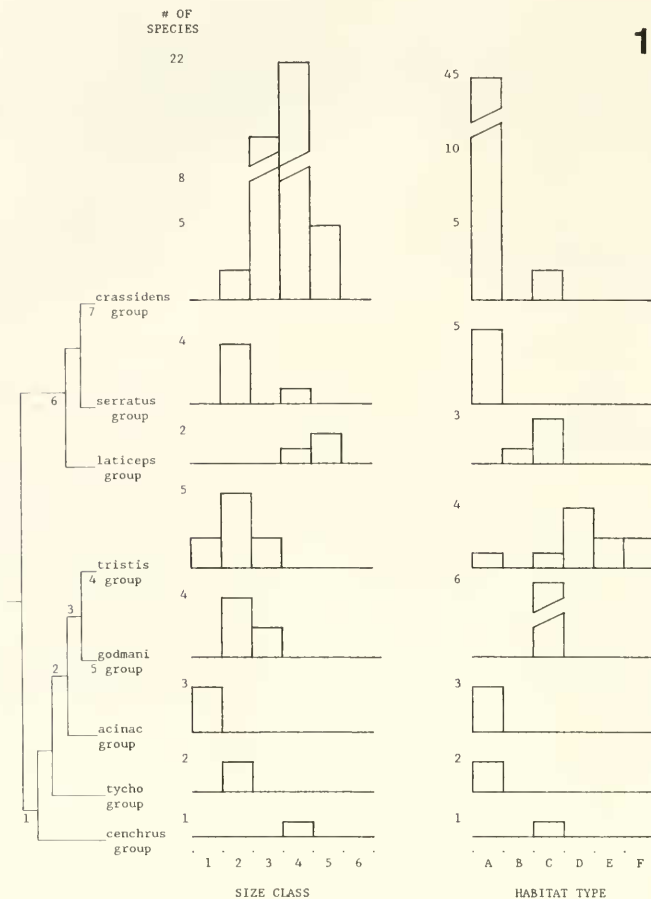
Fig. 1. Frequency histograms showing numbers of species in each species group of *Eustilicus* in Mexico, Guatemala and the United States with certain attributes, and how this relates to the hypothesized phylogeny for the genus. SIZE CLASS. Intervals for the measure of body size employed (mean for head length + pronotal length) were: 1 >1.76; 2 >2.00; 3 >2.24; 4 >2.46; 5 >2.70; 6 >2.94 mm. Differences in means between any two species placed in adjoining intervals were statistically significant at the .001 level (student's *t*-test). HABITAT

oldest ones) from the ancestral niche— thought to be ground litter in mesic forests at middle elevations. This scenario was based in part on the observation that most species which have maintained the ancestral way of life for the genus belong to the crassidens group (Fig. 1). It was also observed (Fig. 1) that if other groups occur in ground litter (serratus, tycho, and acinac groups), then they are found for the most part at higher elevations than the crassidens group (serratus and tycho groups), or they are smaller in size (acinac group). Indeed, compared to the crassidens group, all the other

groups occupy either the high or the low end of the range for body size in the genus (Fig. 1). Other interactions were also proposed, such as displacement of the tristis group by the godmani group from the ancestral habitat for the tristis + godmani group clade.

One difficulty with interpretation of the ecological data was that the character consistency indices for these traits were quite low, ranging from 0.38 for habitat type to just 0.12 for body size. This indicated that the fit of these data onto the cladogram was poor, and that perhaps an evolutionary interpretation of the patterns was not war-
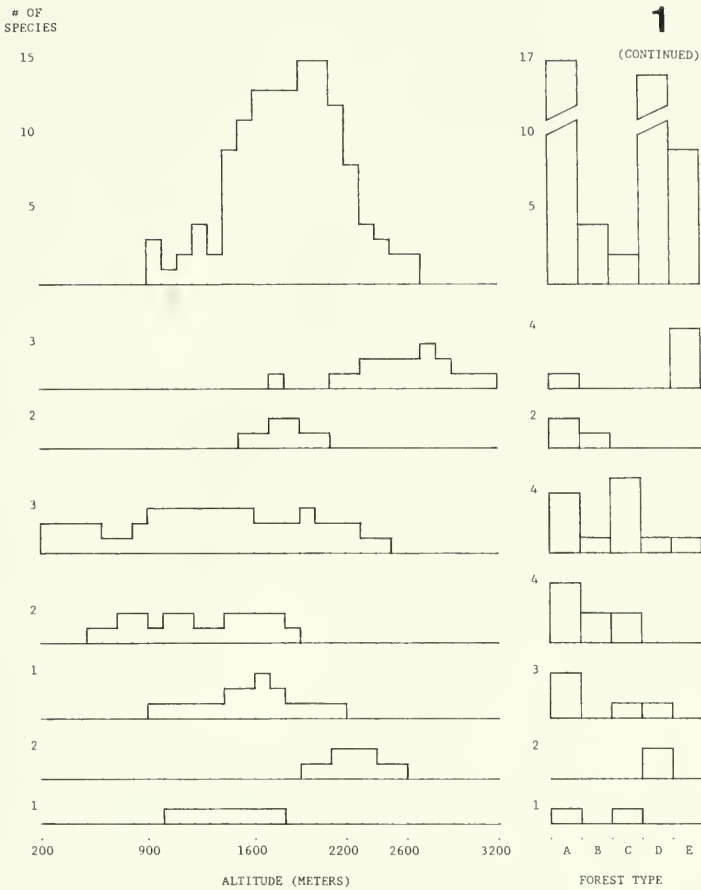
TYPE. A, ground litter; B, treefall litter; C, streamside litter; D, flotsam on riverbanks; E, arroyo litter; F, caves. ALTITUDE. The elevational range of each species was noted and the species was counted present in each interval over that range. FOREST TYPE. A, mesophytic forest, including tropical semideciduous forest and oak-pine forest of tropical aspect; B, tropical evergreen forest; C, arid woodlands, including oak scrub, thorn forest, arid tropical scrub and juniper grassland; D, oak-pine forest of temperate aspect; E, cloud forest.

ranted. A problem with the character consistency index is that it tends to be low if the number of taxa examined is high, irrespective of other considerations (Archie 1989). In the present study, a cladistic randomization test employed by Liebherr and Hajek (1990) was used to investigate whether the ecological patterns of distribution observed in *Eustilicus* deviate statistically from patterns generated at random.

The test which Liebherr and Hajek (1990) employed is as follows. First, a transformation series is established for the natural history trait in question. Secondly, the oc-

currences of the various character states are mapped onto a reconstructed phylogeny for the group, and the minimum number of character state changes over the tree is computed using Wagner parsimony (= Farris optimization). The number of changes is then calculated again using Camin-Sokal parsimony. Reversals are allowed under Wagner parsimony, but not under Camin-Sokal rules. Thirdly, for each character the character states in the data set are sampled without replacement and reassigned randomly to the terminal taxa. The number of character state changes over the tree is then
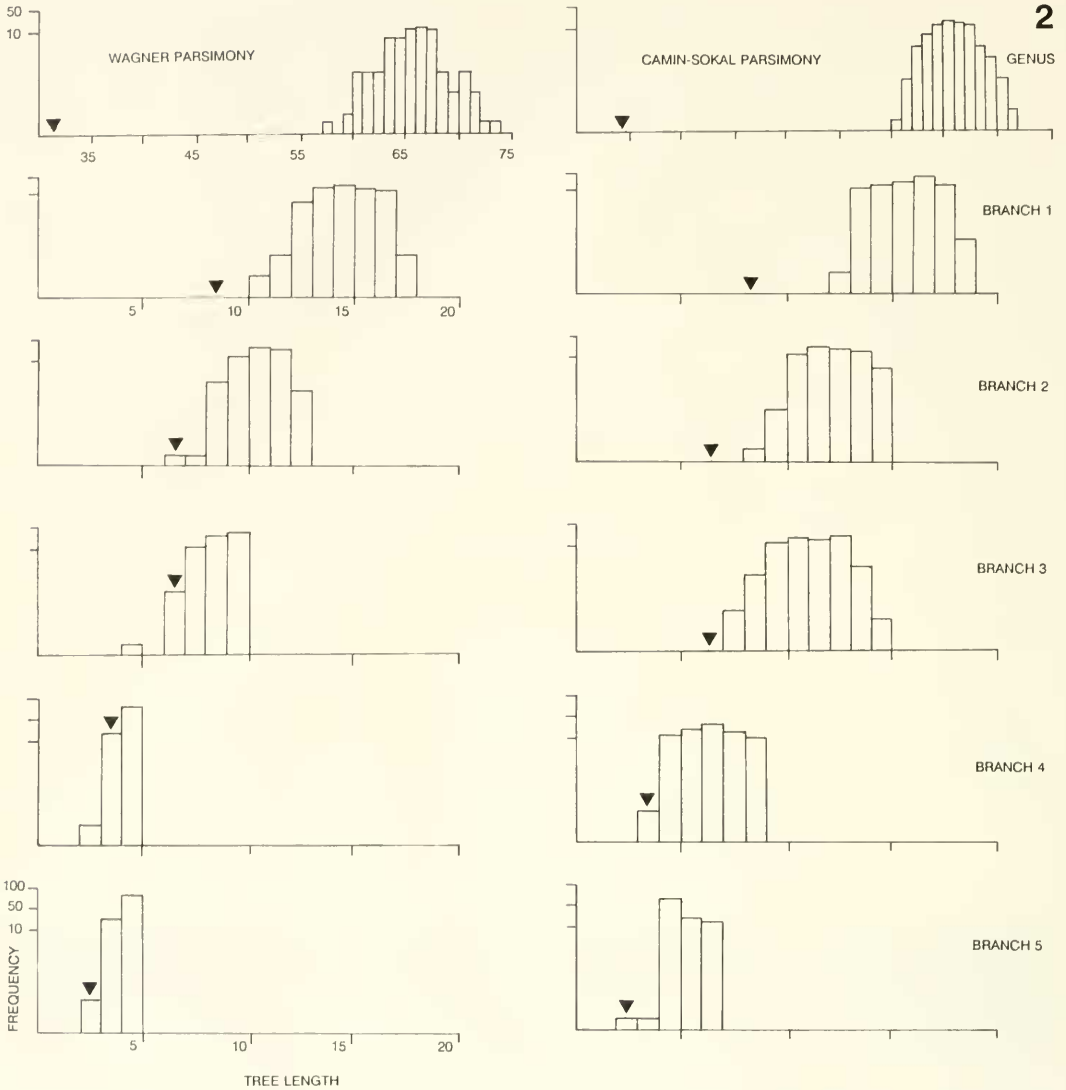
Fig. 2. Frequency histograms showing the number of times (vertical axis) a particular tree length (horizontal axis) was obtained when the data about altitudinal range were randomized, then superimposed upon a cladogram for the genus *Eustilicus,* etc., and the number of character state changes computed using Wagner or Camin-Sokal Parsimony. The number of character state changes calculated using the original data about altitudinal range is indicated by a triangle.

determined for the randomized data. The third step is repeated 100 times and a frequency histogram constructed showing the distribution of values for tree length obtained using the randomized data sets (e.g. Fig. 2). If the length of the tree calculated using the original data is less than 95 of the tree lengths computed using the random-

ized data, it is likely that changes in the character took place in a non-random fashion.

According to Liebherr and Hajek (1990), a statistically significant result using Wagner parsimony indicates that there has been a degree of habitat constancy. A positive result using Camin-Sokal parsimony indi-

cates that reversals for the trait have been uncommon during evolution of the group, and it may be appropriate to invoke the displacement of one taxon by another as the cause of the pattern. This is because according to various taxon displacement models (e.g. taxon cycles, Wilson 1961; taxon pulses, Erwin 1979) the new groups which ultimately replace the older ones arise in the ancestral niche for the group as a whole, so that reversals in ecological traits occur rarely if ever.

In this study, the approach of Liebherr and Hajek (1990) was extended to a consideration of more than one ecological trait, and applied at several taxonomic levels. The problem was also examined of how to treat species that live in more than one habitat, or otherwise have broad ecological preferences.

Materials and Methods

Characters were referred to by number (e.g. character 1) and character states by a small letter (1a). For character state trees with branches, all of the character states on one branch were assigned letters sequentially (1a, 1b, 1c, 1d), then the first character state on the second branch was assigned the next letter in the sequence in capitals and a small letter indicating the character state immediately ancestral to it (1Eb). The characters were:

1. Habitat type: ground litter (A); streamside litter (B); flotsam on riverbanks (C); arroyo litter (D); caves (Eb); treefall litter (Fb).

2. Altitudinal distribution: from above 1400 m to 1800 m (A); above 1800 m to 2100 m (B); above 2100 m (C); 900 to 1400 m (Da); below 900 m (E).

3. Forest type: mesophytic forest (including tropical semideciduous forest and oak-pine forest of tropical aspect) (A); cloud forest (B); dry tropical and subtropical forest (comprising tropical deciduous forest, tropical scrub, oak-acacia scrub, and oak-juni-

per scrub) (Ca); oak-pine forest of temperate aspect (Da); wet tropical forest (Ea).

4. Body size, as indicated by the mean of the head length + pronotal length: up to 2.24 mm (A); up to 2.46 mm (B); up to 2.70 mm (C); up to 2.94 mm (D); more than 2.94 mm (E); 2.00 mm or less (Fa).

Details about these traits will be presented in the revision. The character state data are given in Table 1. The species treated in this study and the group to which each belongs are: cenchrus group, species 1; tycho group, species 2–3; acinac group, species 4–6; godmani group, species 7–14; tristis group, species 15–24; laticeps group, species 25–27; serratus group, species 28–32; crassidens group, species 33–91. The fully resolved tree will be illustrated in the revision. The standardized set notation for this tree (Felsenstein 1986) is:

$$((1,((2,3),(((4,5),6),((((7,8),(9,(10,11)))),((12,13),14)),((15,(16,17)),(((18,19),(20,(21,(22,23)))),24)))))),(((25,26),27),((29,(28,(30,(31,32)))),(((33,(((34,35),36),(37,38))),39),(((42,43),(44,45)),((41,(46,((((47,48),(49,50)),51),52))),(((((53,54),55),56),(((40,57(57,58)),(59,((60,61),(62,63)))),((64,((65,66),67)),(68,69)))))))),(77,(((70,((((71,72),(73,74)),75),76)),(78,79)),(80,((82,(81,83)),((84,(85,86)),((87,88),((89,91),90)))))))))))))$$

An assumption in this study was that the phylogeny is correct. Other assumptions were that the character transformation series are ordered properly and the ancestral condition for each character is known. The latter assumption may not hold for body size because based on Wagner parsimony state C is the ancestral condition, while based on outgroup comparison condition A is ancestral.

To implement the randomization test, the original letter coded data were randomized 100 times using the Randomiz computer program (J. W. Archie, version dated 11/22/89). Each set of randomized data was then additively binary coded using the Factor program in the Phylip computer package (J. Felsenstein, version 2.9). The Mix pro-

Table 1. Character state matrix for selected species of *Eustilicus*. Optimal character state under Wagner parsimony is underlined once; least optimal character state under Wagner parsimony (if different) is underlined twice.

Species	1	2	3	4	Species	1	2	3	4
1	B	A, Da	A, Ca	C	24	B	A	B	B
2	A	B,C	Da	A	25	B, Fb	A	A	D
3	A	C	Da	A	26	B	A	Ea	D
4	A	A	A	Fa	27	B	A, B	A	C
5	A	A, B, C, Da	A, Ca, Da	Fa	28	A	C	B	A
6	A	A	A	Fa	29	A	A	A	C
7	B	Da	Ea	A	30	A	C	B	A
8	B	E	Ea	B	31	A	C	B	A
9	B	Da	A, Ca	A	32	A	C	B	A
10	B	A, Da, E	A, Ca	A	33	B	Da	B	B
11	B	A, Da	Ea	Fa	34	Fb	Da	Ea	C
12	B	A	Ea	A	35	Fb	Da	Ea	B
13	B	A	A	A	36	B	Da	Ea	C
14	B	B	A	B	37	B	Da	Ea	E
15	B	Da	Ea	A	38	B	A, Da	Ea	E
16	A, Eb	Da, E	Ca	A	39	A	C	B	C
17	A, Eb	A, B, C, Da, E	A, Ca	A	40	Fb	E	Ea	B
18	D	A, B, C, Da	Da	Fa	41	A	B	A	B
19	D	B	A	Fa	42	A	B	B	D
20	C	E	A	A	43	A	B	A	C
21	C	A, Da	Ca	B	44	A	B	A	C
22	C	Da	Ca	A	45	A	A	B	B
23	C	Da	Ca	A	46	A	B	A	B
47	A	A	A	B	70	A	A, B, Da	Ca, Da	C
48	A	A, Da	A, Ea	B	71	A	B	Da	D
49	A	A	A	C	72	A	B, C	Da	C
50	A	A	A	D	73	A	A	A	D
51	A	A	A	C	74	A	B	Da	C
52	A	Da	A	B	75	A	A	Da	C
53	A	B	B	C	76	A	A, B	A	C
54	A	A	B	C	77	A	B	B	B
55	A	A, B	B	B	78	A	C	Da	C
56	A	Da	B	B	79	A	A, B, C	Da	C
57	Fb	Da	Ea	B	80	A	B	Da	D
58	Fb	Da	Ea	B	81	A	B, C	Da	B
59	A	A	A, Ea	C	82	A	B	B	B
60	A	Da	B	C	83	A	C	Da	B
61	A	A	A	B	84	A	C	Da	B
62	A	Da	Ea	A	85	A	B, C	Da	B
63	A	Da	Ea	A	86	A	C	Da	B
64	B	A	Ea	C	87	A	B	A	C
65	Fb	Da	Ea	C	88	A	B	A	B
66	B	A, B	Ea	D	89	A	A, B, C	A, Ca, Da	C
67	B	A, Da	Ea	C	90	A	C	Da	C
68	B, Fb	A, Da	Ea	C	91	A	A, B	Da	C
69	Fb	A	Ea	D					

gram in Phylip was then used to compute tree lengths, first under Wagner parsimony (the default in Mix) and then under Camin-Sokal parsimony (CS option), the tree being input with the U option.

If a species exhibited more than one state of a character, parsimony was used to choose which state to include in the data set. This was done by computing the length of tree using the original data with the characters in question coded as missing "?" for the relevant species. It was then determined which state of the character in question would least increase the length of the tree; i.e. with respect to the altitudinal range of species 1, state A was selected over state Ea for inclusion in the data set because one less step was added to the length of the entire tree. In two instances the optimal character state was not one of the states exhibited by those species: e.g. in species 9 and species 10 the optimal character state for forest type was Ea (tropical rainforest), but these two species do not occur in that kind of forest, so state A was selected instead. In five instances different character states proved to be optimal depending upon whether the calculation was done using Wagner or Camin-Sokal parsimony. For the forest preference of species 59, using Wagner parsimony the fewest character state changes were required if state Ea was selected, but using Camin-Sokal parsimony it was preferable to choose state A; in species 16 and species 17 state Eb of character 1, in species 70 state A of character 2, and in species 76 state A of character 2 were optimal under Camin-Sokal parsimony, but not under Wagner parsimony (Table 1).

Selecting character states on the basis of the most parsimonious alternative could introduce a bias for a statistically significant result because homoplasy owing to the existence of species with broad ecological preferences is not taken into account. This possibility was examined by repeating the tests for the worst possible case, e.g. if a species exhibited two or more states of a character,

that state was selected for inclusion in the data set which most increased the length of the tree. In five instances different character states were least optimal depending on how the calculation was done: i.e., in species 10 state E of character 2, in species 11 state A of character 2, in species 59 state Ea of character 3, in species 89 state C of character 2, and in species 91 state A of character 2 proved to be least optimal under Camin-Sokal parsimony, but not using Wagner parsimony (Table 1).

Tests were done first on the genus as a whole, and then at several taxonomic levels within the genus: e.g. on the clade comprised of cenchrus + tycho + acinac + tristis + godmani groups, on the acinac + tristis + godmani group clade, etc. (Table 2). Testing was not extended below the species group level.

Results

Results obtained using the original data.—For the genus as a whole, the tree length computed using the original data for altitudinal range, forest type and body size was greater under Camin-Sokal parsimony than Wagner parsimony (Tables 2–3). This was because the number of character state changes for each of these traits could be reduced by invoking reversals in the laticeps + serratus + crassidens group clade. Such was not the case in the cenchrus + tycho + acinac + godmani + tristis group clade, or among subordinate taxa in this clade. When each of these taxa was tested alone, for all three traits the length of the tree was usually the same whether the calculation was done using Wagner or Camin-Sokal parsimony. However, for habitat type the tree for the tristis + godmani group clade was one step longer under Camin-Sokal parsimony. This is because it is most parsimonious if state B is taken to be the ancestral condition in the clade, but under Camin-Sokal parsimony it is necessary to postulate the existence of a hypothetical ancestor having state

Table 2A.   Length of a cladogram for the genus *Eustilicus* for each of four ecological traits based upon the original data, followed in parentheses by the number of tree lengths of this number of steps or less obtained using 100 sets of randomized data. Lengths calculated using Wagner parsimony (= Farris optimization). Optimal character state selected for those species which exhibit more than one state of a character. Branches: 1, cenchrus + tycho + acinac + godmani + tristis group; 2, acinac + godmani + tristis group; 3, tristis + godmani group; 4, tristis group; 5, godmani group; 6, laticeps + serratus + crassidens group; 7, crassidens group. NS, not statistically significant at the 95% confidence level.

| Clade | Ecological Traits | | | |
	Habitat Type	Altitudinal Range	Forest Type	Body Size
Genus	13 (0)	32 (0)	27 (0)	36 (0)
Branch 1	5 (0)	9 (0)	9 (0)	9 (7) NS
Branch 2	4 (0)	7 (1)	8 (2)	7 (6) NS
Branch 3	3 (0)	7 (7) NS	8 (6) NS	6 (35) NS
Branch 4	3 (0)	4 (25) NS	5 (12) NS	3 (7) NS
Branch 5	0 (100) NS	3 (3)	3 (88) NS	3 (100) NS
Branch 6	8 (0)	23 (0)	18 (0)	27 (0)
Branch 7	7 (0)	20 (0)	16 (0)	24 (0)

Table 2B.   As in Table 2A, except least optimal character state selected for those species which exhibit more than one state of a character.

| Clade | Ecological Traits | | | |
	Habitat Type	Altitudinal Range	Forest Type	Body Size
Genus	15 (0)	55 (0)	37 (0)	36 (0)
Branch 1	6 (0)	19 (22) NS	13 (3)	9 (6) NS
Branch 2	5 (0)	16 (21) NS	11 (13) NS	7 (4)
Branch 3	4 (0)	14 (34) NS	10 (12) NS	6 (35) NS
Branch 4	4 (0)	10 (52) NS	5 (10) NS	3 (9) NS
Branch 5	0 (100) NS	4 (25) NS	5 (78) NS	3 (100) NS
Branch 6	9 (0)	36 (0)	24 (0)	27 (0)
Branch 7	7 (0)	33 (0)	22 (0)	24 (0)

A, hence the extra character state change (Fig. 3).

Results obtained using the randomized data.—For the entire genus, and for the laticeps + serratus + crassidens group clade, and the crassidens group by itself, the length of the tree computed using the original data was for all four traits at least ten steps shorter than when the length was determined using randomized data (e.g. Fig. 2). This was regardless of whether Wagner or Camin-Sokal parsimony was used or which character state was assigned to species that exhibit more than one state of a character (Tables 2–3). It can be concluded that all shifts in ecological preference involving these taxa took place in a non-random fashion. For habitat type and body size, the results obtained concerning the cenchrus + tycho + acinac + godmani + tristis group clade, and subordinate taxa in this clade were also straightforward. In all but one clade the length of the tree computed using the original data about habitat type was at least one step shorter than when the length was determined using randomized data, irrespective of the conditions of the test (Tables 2–3). The godmani group was the exception; this is because all members of the godmani group live in the same habitat. Thus, the test results indicate that all changes in habitat type involving the cenchrus + tycho + acinac + godmani + tristis group clade also occurred in a non-random fashion. As for

Table 3A.   As in Table 2A, except lengths obtained using Camin-Sokal parsimony.

| Clade | Ecological Traits | | | |
	Habitat Type	Altitudinal Range	Forest Type	Body Size
Genus	13 (0)	35 (0)	32 (0)	48 (0)
Branch 1	5 (0)	9 (0)	9 (0)	9 (7) NS
Branch 2	4 (0)	7 (0)	8 (2)	7 (4)
Branch 3	4 (0)	7 (0)	8 (2)	6 (35) NS
Branch 4	3 (0)	4 (3)	5 (12) NS	3 (11) NS
Branch 5	1 (100) NS	3 (1)	3 (68) NS	3 (100) NS
Branch 6	8 (0)	26 (0)	23 (0)	39 (0)
Branch 7	7 (0)	24 (0)	21 (0)	34 (0)

Table 3B.   As in Table 3A, except least optimal character state selected for those species which exhibit more than one state of a character.

| Clade | Ecological Traits | | | |
	Habitat Type	Altitudinal Range	Forest Type	Body Size
Genus	17 (0)	65 (0)	40 (0)	48 (0)
Branch 1	8 (0)	21 (27) NS	13 (3)	9 (4)
Branch 2	7 (0)	18 (39) NS	11 (9) NS	7 (4)
Branch 3	7 (0)	16 (47) NS	10 (12) NS	6 (27) NS
Branch 4	6 (0)	10 (40) NS	5 (8) NS	3 (12) NS
Branch 5	1 (100) NS	6 (56) NS	5 (68) NS	3 (100) NS
Branch 6	9 (0)	44 (0)	27 (0)	39 (0)
Branch 7	7 (0)	41 (0)	25 (0)	34 (0)

body size, in every test on the cenchrus + tycho + acinac + godmani + tristis group clade or on subordinate taxa in this clade there were more than five instances where the length of the tree obtained using randomized data was the same as or less than the length calculated using the original data (Tables 2–3). Therefore, all changes in body size involving this clade could have taken place at random.

For altitudinal range and forest type, the results concerning the cenchrus + tycho + acinac + godmani + tristis group clade were not so simple. When the optimal character state was chosen for species which exhibit more than one state of a character, for the entire clade the length of the tree computed using the original data about altitudinal range was two to four steps less than the shortest tree length obtained using randomized data (Fig. 2). For the acinac + godmani + tristis group clade there was some overlap between the length computed using the original data and the randomized data for altitudinal range when the test was done using Wagner parsimony (Fig. 2). For the godmani + tristis group clade, and the tristis group, there was no significant deviation from randomness observed for altitudinal range when the test was done using Wagner parsimony; in contrast, a positive result was obtained for both clades when the test was done using Camin-Sokal parsimony. As for the godmani group, a departure from randomness for altitudinal range was observed, but under Wagner parsimony the deviation was only marginally significant. When that character state which most increased the length of the tree was assigned to species that exhibit more than one state of a character no deviation from randomness was observed for altitudinal range at any taxonomic level in the cenchrus + tycho + aci-

3

species	altitudinal range	habitat type
7	Da	B
8	E	B
9	Da	B
10	Da	B
11	Da	B
14	B	B
12	A	B
13	A	B
15	Da	B
16	Da	A (Eb)
17	Da	A (Eb)
24	A	B
18	A	D
19	B	D
20	E	C
21	Da	C
22	Da	C
23	Da	C

Fig. 3. Hypothesis of phylogeny for certain species in the godmani and tristis groups of the genus *Eustilicus,* showing character state data for altitudinal range and habitat type. Points at which it is most parsimonious to postulate changes in habitat type are indicated by the letter representing the new character state. Parentheses indicate the optimal condition under Camin-Sokal parsimony.

nac + godmani + tristis group clade (Tables 2–3B).

Results concerning forest type were similar to those obtained for altitudinal range, except that for the tristis and godmani groups no deviation from randomness was observed for this trait (Tables 2–3A). In contrast, a marginally significant deviation from randomness was obtained for the cenchrus + tycho + acinac + godmani + tristis group clade as a whole when the least optimal character states were included in the data set (Tables 2–3B).

DISCUSSION

The impetus for this study was the possibility that an evolutionary interpretation of the ecological data for *Eustilicus* was not warranted because the character consistency indices for the traits in question were very low. This concern proved to be unfounded

because when randomization tests were carried out, for the genus as a whole a considerable gap was always observed between the values for tree length obtained using randomized data and the original data, even though the values of "ci" ranged from just 0.12 for altitudinal range to 0.38 for habitat type. Thus, the character consistency index is not a good indicator of whether a particular character is distributed in a non-random fashion on a cladogram.

The results of the randomization tests at first sight appeared to be entirely consistent with the premise that there have been shifts in habitat type, altitudinal range, forest preference, and body size in the cenchrus + tycho + acinac + godmani + tristis group clade away from that of the crassidens group. For habitat type, the test results also seemed to provide unequivocal support for the proposal that there have been interactions between the tristis and godmani groups which led to shifts in habitat type in the tristis group. Some issues arose during the analysis which suggest that some of the results should be treated with caution.

Effect of the number of repetitions.—Body size was coded such that no species could exhibit more than one state of the character, so the results for body size should have been the same in tests 1 and 2 (Table 2), and in tests 3 and 4 (Table 3). In regards to the cenchrus + tycho + acinac + godmani + tristis group clade, a non-significant result was obtained in test 3 (Table 3A), a marginally significant result in test 4 (Table 3B). This indicates that at least in marginal cases, it is necessary to increase the number of repetitions.

Effect of different strategies for selecting character states when a species exhibits more than one state of a character.—The use of parsimony to choose between alternative character states for species which exhibit more than one condition of a character has the advantage that it is consistent with the outgroup criterion for selecting the primitive condition of a character. Liebherr and

Hajek (1990) used ecological criteria for this purpose, e.g. for each species in the *Platynus jaegeri* group which has a wide elevational range, the lowest elevational interval where that species occurs was selected because this reflects "the tolerance of the species for marginal and/or oscillating conditions." A difficulty with their approach is that the procedure is arbitrary and contentious (it probably depends on the locale whether conditions at lower elevations are less predictable than at higher elevations). Also, this approach is not applicable to all traits, and could introduce biases in favour of one result or another which are not immediately apparent. The use of parsimony avoids these problems, but there are other difficulties. Randomization tests done using Camin-Sokal and Wagner parsimony will not always be entirely comparable with one another because the character state that is optimal under Wagner parsimony may not be optimal under Camin-Sokal parsimony. In the present study there were only three instances of this sort. A more serious difficulty was the bias introduced in favour of a positive result. An attempt to counteract this bias by selecting the least optimal character states for the tests was too successful; then for most traits statistically significant results were obtained only at the highest taxonomic levels. What is required is some less extreme strategy for selecting character states.

Nonetheless, the results of the "worst case" tests cast doubt on the findings of statistically significant deviations from randomness for altitudinal range and forest preference in the cenchrus + tycho + acinac + godmani + tristis group clade. This is because so many species are found over a broad elevational range, and/or in more than one type of forest.

Effect of a significant test result at one taxonomic level on results at another taxonomic level—Using Wagner parsimony, a marginally significant departure from randomness for altitudinal range was obtained for the godmani group because one clade in

this group tends to be found at higher elevations than the other (Fig. 3). However, the deviation from randomness was not large enough, or perhaps there were not enough taxa in this clade to produce a statistically significant result for the tristis + godmani group clade as a whole. Evidently, a negative result at one taxonomic level does not rule out the possibility of a statistically significant deviation from randomness at a subordinate taxonomic level. Conversely, if there is a large enough deviation from randomness in just one of several clades, this can result in a statistically significant result at a more inclusive taxonomic level. Thus, the marked deviation from randomness for body size in the laticeps + serratus + crassidens group clade could account entirely for the finding of a statistically significant pattern for the genus as a whole because the cenchrus + tycho + acinac + godmani + tristis group clade does not show a departure from randomness for body size. However, the pattern of complementarity for body size evident in Fig. 1 appears to be decisive in showing that there have been shifts in body size in the cenchrus + tycho + acinac + godmani + tristis group clade away from that of the crassidens group.

Conclusions

Results of the randomization test support the premise that some shifts in habitat type, altitudinal range, forest preference, and body size in the genus *Eustilicus* were due to the displacement of one taxon by another. The test does not always allow one to identify the taxa between which interactions took place. This difficulty becomes apparent when tests are carried out at more than one taxonomic level. Plotting the natural history data in various ways to reveal complementary patterns of distribution (e.g. Fig. 1; fig. 71, Allen and Ball 1980; fig. 144, Whitehead 1976) effectively resolves this problem.

A statistically significant deviation from randomness for one ecological trait at some taxonomic level in *Eustilicus* was often ac-

companied by a negative result for another trait. Also, a significant result for a trait at one taxonomic level was not necessarily reflected at higher or subordinate taxonomic levels. This indicates that more intensive analyses are required before concluding as Liebherr and Hajek (1990) have done that in many instances, shifts in habitat type, etc. previously attributed to the displacement of one taxon by another, are actually owing to chance, or to climatic changes and nothing more.

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